Preimaginal Environment Influences Adult Flight in *Cydia molesta* (Lepidoptera: Tortricidae)

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ABSTRACT Dispersal of adult tortricid moths between habitats may have important consequences for pest management in orchards, but little is known about how flight parameters are affected by environmental conditions during preimaginal development. The influence of changing temperature and photoperiod (both singly and in combination) as well as of larval crowding and food deprivation were investigated in *Cydia molesta* Busck (Lepidoptera: Tortricidae), a species that has been found to disperse after peach harvest and colonize pome fruit orchards. Comparative assessments of flight parameters were made on a computer-linked flight mill and life history traits were evaluated. A significant increase in flight performance was correlated with preimaginal exposure to decreasing photoperiod. In addition, pupal development was delayed and larger individuals emerged, but preimaginal survivorship was reduced. Decreasing and increasing temperature regimens and increasing photoperiod did not influence adult flight. Larval crowding was associated with increased flight, but the differences were not statistically significant. Food deprivation was associated with accelerated preimaginal development, lower pupal weight, less fecund adults, and reduced flight. We propose that the main factor eliciting dispersal in this tortricid is decreasing photoperiod.

KEY WORDS dispersal, preimaginal environment, temperature, photoperiod, *Cydia (Grapholita) molesta*

ALL PHYTOPHAGOUS INSECTS DISPERSE to some extent, whether to another part of the same plant like scale insects (Ben-Dov and Hodgson 1997) or as a part of an obligate migration of thousands of kilometers like the Monarch butterfly, *Danaus plexippus* L. (Lepidoptera: Danaidae) (Gibo 1996). However, most insects are facultative dispersers, moving relatively short distances in response to decreasing habitat quality. Insect dispersal may occur directly in response to biotic factors such as resource depletion, reduced host quality, increased competition, or predation. Alternatively, dispersal may be elicited by abiotic factors, such as temperature or photoperiod, that are either directly indicative of habitat quality or that are temporally synchronous with biotic habitat decline (Rankin and Burchstead 1992).

Most insects disperse to new habitats as adults. Therefore, sensitivity to environmental conditions indicative of habitat quality encountered during preimaginal development may be critical for adult dispersal and subsequent success. Adaptations for dispersal may be behavioral. For example, whiteflies reared on senescing plants exhibited greater takeoff rates and flight initiation than individuals reared on vegetative plants (Blackmer and Byrne 1993). In contrast, some species display gross morphological dispersal adaptations, such as alate forms of aphids (Wratten 1977). More subtle morphological changes in size or wing loading may also be correlated with greater dispersal capacity.

Little is known about the influence of preimaginal environment on adult flight in tortricid moths, despite their economic importance. Dispersal of the oriental fruit moth, *Cydia molesta* Busck (Lepidoptera: Tortricidae), has become an increasingly important issue because of the economic importance of this species in pome-fruit after stone-fruit harvest (Pollini and Bariselli 1993). Although typically considered to be a key pest of peach, late generations of this multivoltine species colonize pome-fruit orchards (Zhao et al. 1989, Pollini and Bariselli 1993). Volatiles from both peach and apple fruit at different stages of maturation, as well as shoots from both trees, are attractive to this species (Natale et al. 2003a, b). Previous studies indicate that, although the majority of *C. molesta* individuals tend to be sedentary, a proportion of the population is capable of considerable interorchard dispersal, with gravid females being the main dispersers (Hughes and Dorn 2002 and references quoted therein). The mechanisms

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underlying this late-season dispersal are unknown and may include both abiotic and biotic factors. The late summer migration of *C. molesta* coincides with declining photoperiod, and to a lesser degree, declining temperature. These abiotic factors may act as dispersal cues. Although the larvae spend their entire preimaginal development concealed in host plant tissue, last-instar larvae are sensitive to decreasing photoperiod for diapause induction (Saunders 1982), indicating that these endophytic stages can respond to changing ambient conditions, including light regimen. Availability of fruit declines during stone-fruit harvest. However, larvae typically use only one fruit for the completion of their development (Rothschild and Vickers 1991). Thus the importance of food shortage may be limited. However, intraspecific preimaginal competition may be marked, with 3, 4, or even more larvae observed in each peach fruit (Balachowsky and Mesnil 1935).

The influence of preimaginal environment on *C. molesta* flight and life history parameters was investigated with the aim of elucidating some key dispersal cues used by this species. Temperature, photoperiod, food deprivation, and larval crowding regimens were simulated, and their effect on preimaginal development and adult flight, longevity, and fecundity was investigated.

Materials and Methods

Insect Rearing. The insects used were descendants of field-collected adults from the Emilia Romana region of Northern Italy. The moths were reared in the laboratory for 40–50 generations before use in this study. Environmental culturing conditions were 26°C, 70% RH, and L16:D8. Adults were collected on the day of eclosion, and equal numbers of male and female moths were placed in oviposition chambers (1,425-cm^3 mesh-bottomed plastic cylinders). Moths were supplied with an excess of food at all times from a reservoir of 10% honey (g)/water (ml) solution with a cotton wool wick. The oviposition chambers were lined with a plastic sleeve, which was replaced daily. Removed sleeves were checked twice daily during the expected hatching period, and neonate larvae (<24 h) were removed and placed singly in covered plastic rearing boxes (8.7 cm^3) containing ≈800 mg (1.8 cm^3) agar-based artificial diet (Huber et al. 1972). The covers of the individual rearing boxes were removed when larvae reached the final instar, and the boxes were placed in a larger plastic box (1,800 cm^3) containing strips of corrugated cardboard. Larvae emerged from the diet and entered the strips to pupate. The cardboard strips were replaced daily. Ten days after larval entry, the strips were opened, and pupae were removed from their cocoons and sexed (Beeke and De Jong 1991). Male and female pupae were kept separately in ventilated plastic boxes (1,800 cm^3). Control moths and moths from all other treatments were reared under these conditions, with the exception of the treatment modifications described hereafter.

Environmental Regimens. Temperature, photoperiod, food deprivation, and larval crowding regimens were simulated. Photoperiod and temperature regimens were applied both singly and in combination to provide six treatments: increasing photoperiod with constant temperature, decreasing photoperiod with constant temperature, increasing temperature with constant photoperiod, decreasing temperature with constant photoperiod, increasing temperature with increasing photoperiod, and decreasing temperature with decreasing photoperiod.

The increasing and decreasing treatments were an inverse of one another, each providing the same amount of thermal- and photostimuli in opposing order. The photoperiod regimens consisted of 14 daily 10-min increments or decrements in the scotophase from a minimum of 8 h (photophase, 16 h) to a maximum of 9 h and 50 min (photophase, 14 h and 10 min). The fluctuating thermoperiod regimens were composed of four thermoperiods: one low, two moderate, and a high thermoperiod, each lasting for 6 h. Each thermoperiod was increased or decreased by 0.2°C daily from a mean high of 21°C (26, 21, and 16°C for high, moderate, and low thermoperiods, respectively) to a mean low of 18.4°C (23.4, 18.4, and 13.4°C for high, moderate, and low thermoperiods, respectively). The photo- and thermostimuli were coordinated in the combination treatments, i.e., the low phase of the thermoperiod treatment was synchronized with the scotophase. The constant temperature and photoperiod regimens were 26°C and L16:D8, respectively.

Each treatment was applied over a 14-d period from neonate larvae aged <24 h onward. Larval development was completed by 98% of larvae in 14 d under culture conditions ($n = 200$). After 14 d, any remaining larvae and subsequent pupae and adults were kept at the same conditions as day 14 of the regimen.

Food deprivation was simulated by providing each larva with ≈400 mg (0.9 cm^3) of food, one-half that provided to all other treatments and the control. Mean food consumption of control larvae was 292 ± 10 mg ($n = 34$). Therefore, sufficient food was provided to complete development. However, larvae were unable to remain burrowed within the food during development. Larvae emerged from the resource at instar three to four onward, and fed externally as the food became depleted.

Larval crowding was simulated by placing two neonate larvae (<12 h old) into each larval rearing box. The volume of food provided (≈1.6 g; 3.6 cm^3) was double that of the noncrowding regimens to ensure that food availability in relation to the control was not compromised.

Flight Performance. A computer-linked tethered flight device was used to compare the influence of different environmental factors on flight. This method has been used in previous studies to measure and compare flight performance in *Cydia* spp. (Dorn et al. 1999, Hughes and Dorn 2002). Mated moths were flown once at 5 d old (calculated as the number of nights since eclosion). The laboratory flight of female *C. molesta* is greatest at 5 d old, whereas male flight

performance is not significantly correlated with age (Hughes and Dorn 2002). Eighty replicates (40 males and 40 females) were tested for each treatment. Male and female moths were tested separately to avoid the confounding influence of interactions between the sexes.

Moths were attached to a tethering pin while held on a mesh stage by gentle suction. The thoracic scales were removed, exposing the sclerite, and the pin was fixed centrally on the thorax using water-based glue. A static test flight was initiated by the application of a gentle air current in all moths both pre- and postattachment. Only moths that were securely attached and displaying wing movement unimpeded by the tethering process were used.

The tethering pin was pushed perpendicularly through a flight arm. The distance between the central axis of the arm and the moth attachment point was 10 cm (revolution circumference, 62.8 cm). The axle pin was placed between two magnets, the magnetic field holding it in a vertical position. A reflector on the flight arm and a computer-linked infra-red receiver mounted on the mill registered each revolution. The sequence of revolutions was interpreted in terms of single flights and breaks. A break was defined as 3 s or longer without a revolution, and a single flight as the period between two breaks. The duration, distance, and speed of each flight were recorded by a computer. Overall flight performance was characterized by two parameters: total distance flown (TDF, the sum of all flights) and longest single flight (LSF, longest unbroken flight made by each individual). In addition, a single flight of >1 km was hypothesized to typify undistracted and persistent flight characterizing interhabitat dispersal (Hughes and Dorn 2002) and the number and percentage of moths making such flights was recorded.

Thirty rigid-tether flight mill units were situated in a climate chamber maintained at 23°C and 70% RH. Flight was monitored over a 16-h period, encompassing three phases of photointensity reflecting the natural light cycle; 4 h of full light (3,750 lux), an 8-h scotophase, and a further 4 h of full light (3,750 lux). The scotophase included 2 h of simulated dusk conditions, 4 h of night (0.1 lux), and 2 h of simulated dawn. Simulated dusk and dawn were composed of a sequence of 10-min steps of decreasing or increasing light intensity from 3,750 to 2,440, 2,210, 1,480, 790, 189, 57, 7.8, 5.6, 3.6, 2.1, 0.5, and 0.1 lux. All lighting was provided by high-frequency daylight spectrum fluorescent lamps.

Moths were removed from the tether after use by the application of gentle pressure on the thorax on either side of the attachment point. Moths flown using this apparatus seemed to be unharmed, and normal copulatory behavior and oviposition was observed after removal from the tether (Hughes and Dorn 2002).

Adult Fecundity and Longevity. Lifetime fecundity, daily oviposition, and longevity of 25 unflown females were recorded for each treatment. Newly emerged females were housed singly in 200-cm^3 clear plastic, mesh-topped cups with two 1-d-old males reared under identical conditions. The males were removed after 48 h. The number of eggs deposited by each female was recorded daily until the individual's death. Fecundity was only recorded in moths that had mated successfully, as indicated by viable egg production.

Preimaginal Life History Traits. For each treatment, the number of individuals completing larval and pupal development, the duration of development, and the number of larvae entering diapause were recorded. Larval development was recorded as the number of days from egg hatch until the larvae entered the pupation strip. Pupal development was recorded as the date of larval entry of the pupation strip until adult eclosion, encompassing any nonfeeding prepupal stage the larva may have undergone. The proportion of diapausing larvae was recorded by counting the unpupated larvae present within the cocoons 10 d after larval entry of the pupation strip. Pupal weight was recorded for a random subsample of 100 individuals (50 males and 50 females) for each treatment.

Statistical Analysis. The duration of larval and pupal development, pupal weight, and flight performance data were analyzed using analysis of variance (ANOVA) and Fisher least significant difference (LSD) tests. This analysis was conducted using SYSTAT Version 8.0 for Windows (SYSTAT 1998). The pupal weights and flight performance data were analyzed using the sex of the moths and the treatment applied as factors. The flight performance data were also rank-transformed before analysis.

The larval and pupal mortality data were analyzed using a general linear model (GLM) with a binomial distribution and a logit link as explained below. This analysis was conducted using Genstat for Windows Version 4.1 (Genstat 5 Committee 1997). The treatment of the larvae and pupae during rearing was used as the explanatory factor. The data analyzed were the number of individuals surviving to pupation, the number of individuals surviving to adulthood, and the number of diapausing individuals. Multiple comparisons were based on *t*-tests between the parameter estimates and are therefore equivalent to LSD tests. These were calculated using the RPAIR procedure of Genstat; for a discussion of these tests see Crawley (1993).

GLMs are a broad class of statistical models, including linear regression and ANOVA for both continuous and categorical response variates. A GLM has three properties: the error structure or random component, the linear predictor or systematic component, and the link function (Crawley 1993). The random component is determined by the type of data being analyzed. For example, if they are binary, such as success or failure, then a binomial distribution is assumed. Alternatively, they may be non-negative counts, in which case a Poisson distribution is assumed. If the data are continuous, a normal or gamma component distribution is assumed. The linear predictor specifies the number of components in the model and is the linear sum of the effects of one or more explanatory

variables. For example, in linear regression, the linear predictor is the sum of two components: the slope (b) and the intercept (a) ($y = a + bx$). However, the exponential model ($y = a + be^x$) is also linear in its parameters, because a new variable z ($z = e^x$) can be created to yield $y = a + bz$ (Crawley 1993). The link function relates the response variable, measured in the data and predicted by the model in fitted values, to the linear predictor. The canonical links are those most commonly applied to a particular error distribution, i.e., "the default" link. For example, the identity link is used for normal errors, the log link is used for poisson errors, logit link for binomial errors, and the reciprocal link for gamma errors. For example, in linear regression, the response variable is modeled directly by the explanatory variable; this is called the identity link.

The lifetime oviposition data were analyzed using ante-dependence modeling (Gabriel 1962, Kenward 1987, Lindsey 1999). This analysis was conducted using Genstat for Windows version 4.1 (Genstat 5 Committee 1997). Ante-dependence modeling estimates the correlation between the observations at different time points and builds this correlation structure into tests for the significance of treatment effects. In Genstat, this analysis is carried out using two Genstat procedures. The first is used to estimate the order to be used in the model. This procedure is called the ANTORDER procedure. It allows the most appropriate error structure for the data to be estimated. Once the order is established, the Anttest procedure is used to estimate treatment effects (Horgan 1996). For the current dataset, an order of three was found to be adequate. In addition, total lifetime oviposition was analyzed with GLM using a Poisson distribution and a log link. The adult longevity data were analyzed using GLM with a gamma distribution and a reciprocal link (Aitkin et al. 1989, Crawley 1993). Multiple comparisons were based on *t*-tests between the parameter estimates and are therefore equivalent to LSD tests. These were calculated using the RPAIR procedure of Genstat; for a discussion of these tests, see Crawley (1993).

Results

Flight Performance. Preimaginal environment had a significant influence on the LSF of the moths (male and female data combined; $F = 2.8$; df = 4,390; $P < 0.05$). Decreasing photoperiod with constant temperature and also with decreasing temperature during larval development resulted in a significantly greater LSF in adults compared with controls (Fig. 1). In contrast, decreasing temperature alone had no significant influence. Increasing photoperiod and temperature alone or in combination were also unrelated to adult flight. Although the crowding regimen displayed an LSF approximately twice as long as that of the control, these differences were not significant. Larval food deprivation did not result in an increased LSF. The LSF parameter was significantly greater in females than in males ($F = 24.4$; df = 1,390; $P < 0.001$). Females flew between two and five times as far as males, dependent on treatment. There was no statistical evidence that the treatments differentially affected the LSF parameter for female and male moths ($F = 0.9$; df = 4,390; $P > 0.05$).

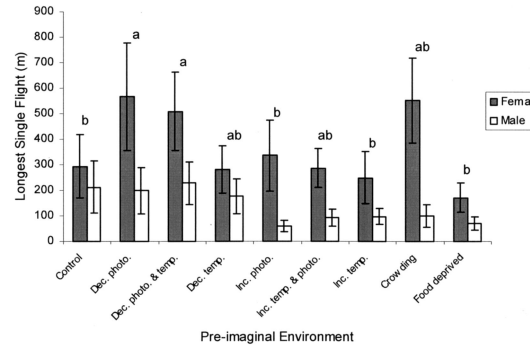

Fig. 1. Influence of preimaginal environment on longest single unbroken flight (LSF) in *C. molesta* ($n = 40$). Error bars indicate SE. Treatments annotated with the same letters (male and female data combined) are not statistically different ($P > 0.05$, Fisher LSD).

The TDF was also influenced by the preimaginal environment ($F = 4.3$; df = 4,390; $P < 0.01$). Moths reared under a decreasing photoperiod with constant temperature flew significantly further than the control. Moths reared in a food-deprived environment flew significantly shorter distances than controls (Fig. 2). The effect of rearing conditions was the same for males and females ($F = 0.4$; df = 4,390; $P > 0.05$). The TDF by females was three to five times higher than of males ($F = 64.9$; df = 1,390; $P < 0.001$).

Female *C. molesta* also flew significantly farther and made a greater number of long flights (>1 km) than males. Ten percent of all female control moths made flights of >1 km compared with 20 and 15% of moths reared under decreasing photoperiod and decreasing photoperiod with decreasing temperature regimens, respectively. Ten percent of female moths reared under increasing photoperiod regimens, both alone and

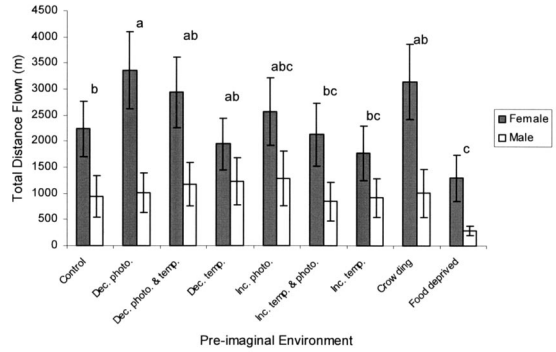

Fig. 2. Influence of preimaginal environment on total distance flown (TDF, sum of all flights) in *C. molesta* ($n = 40$). Error bars indicate SE. Treatments annotated with the same letters (male and female data combined) are not statistically different ($P > 0.05$, Fisher LSD).

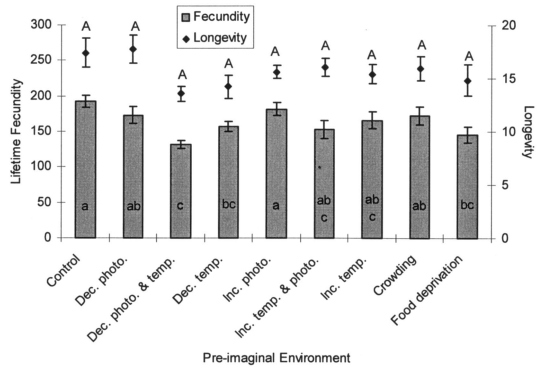

Fig. 3. Lifetime fecundity (eggs per female) and longevity of females (days) in relation to preimaginal environment in *C. molesta* ($n = 25$). Error bars indicate SE. Treatments annotated with the same letters are not statistically different ($P > 0.05$, Fisher LSD or equivalent).

in conjunction with increasing temperature, and 7.5% of the increasing and decreasing temperature regimens made flights of over 1 km. Fifteen percent of crowded regimen moths and only 5% of food-deprived female moths made such flights. In male moths, 7.5% of control moths made long flights, and no other treatment achieved a greater percentage of long fliers.

Adult Fecundity and Longevity. The total number of eggs laid during the lifetime of the female moths was significantly influenced by preimaginal environment (deviance ratio 3.0; df = 8,179; $P < 0.01$). Moths reared under decreasing photoperiod with decreasing temperature or under decreasing temperature alone as well as those reared under food-deprived conditions laid significantly fewer eggs than control moths (Fig. 3).

In addition, when the daily pattern of egg laying was analyzed using ante-dependence modeling, significant differences were seen among the treatments (χ^2 524; df = 173; $P < 0.001$). In both the decreasing photoperiod and crowded treatments, the oviposition period was longer than the control, with significantly more eggs laid on days 14, 15, and 16 than in any other treatment, including the control ($P < 0.05$).

There were no significant differences in moth lifespan among the treatments (deviance ratio, 0.11; df = 4,95; $P > 0.05$; Fig. 3). The mean age at death estimated from the parameter estimates of the GLM was 17.4 d.

Preimaginal Life History Traits. Preimaginal environmental conditions significantly influenced both the proportion of larvae-forming pupae (deviance ratio, 11.2; df = 1; $P < 0.001$) and the proportion of pupae emerging as adults (deviance ratio, 13.1; df = 1; $P < 0.001$; Table 1). Larval and pupal mortality was significantly greater than the control in all treatments except in the decreasing temperature and food-deprived regimens. The proportion of larvae entering diapause was <0.03% for all treatments, and there were no significant differences among the treatments (deviance ratio, 0.7; df = 1; $P > 0.05$).

The larvae that developed successfully showed significant differences in the time taken for development in relation to rearing conditions ($F = 471.5$; df = 8,1319; $P < 0.001$). All treatments involving decreasing or increasing temperature (both in combination with photoperiod and alone) resulted in a significantly longer larval development period (Table 1). In contrast, food deprivation was associated with significantly accelerated larval development.

The duration of the pupal stage also differed significantly in relation to rearing conditions ($F = 24.8$; df = 8,1319; $P < 0.001$). The pupae resulting from larvae reared under control conditions developed more quickly than all other treatments, with the exception of increasing temperature with constant photoperiod and food deprivation (Table 2).

Preimaginal environment had a significant effect on pupal weight ($F = 6.7$; df = 4,490; $P < 0.001$). Female pupae resulting from larvae reared under decreasing or increasing photoperiod with constant temperature conditions as well as those from crowded conditions were significantly heavier than control pupae ($P < 0.05$). Female pupae reared under decreasing photoperiod with decreasing temperature were significantly lighter than controls ($P < 0.05$). Male pupae reared under decreasing photoperiod with constant temperature were significantly heavier than controls ($P < 0.05$), whereas those reared under decreasing photo-

Table 1. Proportion of larvae entering diapause, proportion of insects completing larval and pupal development, and duration of development (mean ± SEM) in relation to preimaginal environment in *C. molesta*

Preimaginal environment	Initial no. larvae	Proportion diapausing	Proportion forming pupae	Proportion emerging as adults	Duration of larval development (days)	Duration of pupal development (days)
Control	200	0.02a	0.59a	0.57a	11.51 ± 0.10e	11.09 ± 0.06c
Decreasing photoperiod	400	0.01a	0.38d	0.34c	11.10 ± 0.09ef	11.74 ± 0.05ab
Decreasing photoperiod and temperature	498	0.01a	0.44bc	0.44bc	16.05 ± 0.11c	11.40 ± 0.06b
Decreasing temperature	500	0.00a	0.52a	0.51a	17.95 ± 0.26a	11.41 ± 0.06b
Increasing photoperiod	400	0.01a	0.39cd	0.35bc	11.57 ± 0.09e	10.90 ± 0.04c
Increasing temperature and photoperiod	360	0.03a	0.35cd	0.32c	15.56 ± 0.17d	11.80 ± 0.08a
Increasing temperature	360	0.03a	0.24e	0.16d	16.60 ± 0.10b	11.84 ± 0.13a
Crowding	200	0.01a	0.46b	0.43b	12.60 ± 0.14e	11.47 ± 0.12b
Food deprivation	238	0.02a	0.55a	0.54a	10.87 ± 0.07f	10.84 ± 0.05c

Means within a column followed by the same letter are not statistically different ($P > 0.05$, Fisher's LSD or equivalent).

Table 2. Pupal weight (mean ± SEM) in relation to preimaginal environment in *C. molesta* (n = 50)

Preimaginal environment	Pupal weight (mg)	
	Female	Male
Control	14.43 ± 0.32b	12.01 ± 0.25b
Decreasing photoperiod	16.92 ± 0.25a	13.12 ± 0.20a
Decreasing photoperiod and temperature	13.72 ± 0.25c	10.34 ± 0.20c
Decreasing temperature	14.79 ± 0.31b	11.97 ± 0.18b
Increasing photoperiod	16.43 ± 0.43a	11.69 ± 0.30bc
Increasing temperature and photoperiod	14.80 ± 0.25b	11.16 ± 0.17c
Increasing temperature	14.24 ± 0.29bc	10.52 ± 0.14c
Crowding	16.49 ± 0.32a	11.44 ± 0.20bc
Food deprived	14.50 ± 0.29b	11.08 ± 0.23c

Means within a column followed by the same letter are not statistically different ($P > 0.05$, Fisher's LSD).

period with decreasing temperature, increasing photoperiod with increasing temperature, and increasing temperature with constant photoperiod regimens were significantly lighter than control pupae ($P < 0.05$; Table 2). Female pupae were significantly heavier than male pupae ($F = 455$; df = 1,490; $P < 0.001$).

Discussion

The elucidation of the factors eliciting *C. molesta* dispersal has important consequences for pest management, particularly in relation to prediction of late-season dispersal from peach to pome fruit orchards. Although decreasing photoperiod, decreasing temperature, larval crowding, and food deprivation during preimaginal development are all temporally synchronous with the dispersal period, only decreasing photoperiod was found to be associated with significantly increased adult flight performance. Decreasing photoperiod at constant temperature had strongest effect on *C. molesta* flight, as both key flight parameters increased, while a decreasing photoperiod at decreasing temperature resulted only in longer single flights but not in longer total distance flown. This response of *C. molesta* to changing abiotic conditions is in contrast with other lepidopteran species. Altered photoperiod during the preimaginal phase had no influence on flight in *Cnaphalocrocis medinalis* Guenee (Lepidoptera: Pyralidae) (Higuchi and Kitamura 1989) and *Plutella xylostella* L. (Lepidoptera: Plutellidae) (Shirai 1993).

Rankin and Burchstead (1992) reviewed the costs of insect migration and found that the most frequently cited effects were increased development time, decreased fecundity, and delayed reproduction. Our study shows that, in *C. molesta*, decreasing photoperiod was correlated with increased development time, increased preimaginal mortality, and delayed reproduction. A delay in reproduction may advantage individuals moving to a new resource, with a later oviposition period allowing increased egg laying after dispersal. In addition to a delay in the onset of reproduction in *C. molesta*, a change in oviposition pattern was observed, because the maximum egg laying period in relation to oviposition initiation was delayed compared with the control. This would further increase the number of eggs deposited after dispersal. Changes in lepidopteran oviposition pattern in relation to preimaginal environment have not been reported previously. Decreasing photoperiod was also correlated with larger *C. molesta* adults, whereas adult size was not influenced in *P. xylostella* (Shirai 1993).

Increasing photoperiod did not influence flight, fecundity, or developmental period, either alone or in combination with increasing temperature. This finding supports the fact that the effects of decreasing photoperiod are not an artifact of changing photoperiod, but that the direction of the change is significant. Furthermore, neither increasing nor decreasing temperature regimens significantly influenced *C. molesta* flight. This is perhaps not unexpected, because temperature is a poor predictor of seasonal change, whereas photoperiod is a more stable and predictable environmental correlate of future conditions. Decreasing temperature was correlated with decreased fecundity, increasing temperature was linked to increased mortality, and both increasing and decreasing regimens were correlated with delayed development. Similarly, decreasing and increasing temperature during development did not modify *C. medinalis* flight (Higuchi and Kitamura 1989). However, *C. molesta*'s response to changing temperature regimens in the preimaginal period was completely different from another tortricid species, *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae) (Gu and Dantharanayana 1992). In this species, increasing temperature during larval development was correlated with a smaller body size of both female and male moths, rendering them capable of prolonged flight.

Larval crowding in *C. molesta* was not significantly associated with increased flight performance, although mean values were higher than in the control. However, larval crowding led to an altered oviposition pattern, with significantly greater oviposition in later life, as described above for moths reared under decreasing photoperiod. In contrast, larval density had no effect on the fecundity of *Mamestra brassicae* L. (Lepidoptera: Noctuidae) (Kazimirova 1996), but was negatively correlated with fecundity in *Earias vitella* (F.) (Lepidoptera: Noctuidae) (Tripathi and Singh 1990). Density-regulated dispersal is common in insects (Price 1997). Larval crowding in *E. postvittana* resulted in adults with greater dispersal ability (Danthanarayana et al. 1982).

Cydia molesta crowding was also associated with increased preimaginal mortality, delayed development, and increased pupal weight. In the simulated crowding regimen, there were sufficient resources to complete development; therefore, there was not an immediate requirement for faster adult emergence. However, the proximity to other larvae may indicate competition for future resources, favoring a longer-term migrational strategy. Therefore, the production of larger adults with greater flight capacity would be beneficial, but the trade-off seems to be increased

preimaginal mortality and development time. Larval crowding has also been shown to increase larval mortality in other lepidopteran species. *Choristoneura rosaceana* Harris (Lepidoptera: Tortricidae) reared at low densities were four times as likely to survive to adulthood compared with those reared at high densities; high larval densities were also correlated with smaller pupae and longer pupal development (Poirier and Borden 1992). Longer developmental time and increased mortality among crowded larvae has also been recorded in *Trichoplusia ni* (Hubner) (Lepidoptera: Noctuidae) (Tignor and Eaton 1986) and *E. vittella* (Tripathi and Singh 1990). In contrast to this study, reduced pupal weight was correlated with larval crowding in *Spodoptera exempta* (Lepidoptera: Noctuidae) (Parker and Gatehouse 1985), *Prodenia litura* (Lepidoptera: Noctuidae) (Zaher and Moussa 1961), and *E. postvittana* (Danthanarayana et al. 1982).

Cydia molesta reared under food-deprived conditions displayed accelerated preimaginal development. This may be an adaptation to host depletion, allowing completion of development before the resource runs out. The trade-offs for quicker development seem to be reduced size, fecundity, and flight. Under this scenario, long-range dispersal to leave a declining resource as a whole seems to be less important than completing development before the immediate host runs out. Neither larval food deprivation nor poor food quality affected flight in *S. exempta* (Walker) (Lepidoptera: Noctuidae) (Parker and Gatehouse 1985). In the field, larval starvation in *C. molesta* summer generations is most likely to occur in conjunction with larval crowding, when a high number of larvae infest one single fruit and compete for a common food resource.

In summary, we simulated late summer conditions in peach-growing countries at the time when *C. molesta* moths colonize pome fruit orchards and exposed preimaginal stages of this herbivore to such typical environments. However, whereas all regimens elicited developmental changes, only decreasing photoperiod experienced in the larval stage was significantly associated with increased flight. Decreasing photoperiod is perceived by last-instar larvae, as has been shown in studies of diapause induction (Saunders 1982). We thus propose that the main factor eliciting dispersal in this tortricid in the field is decreasing photoperiod. Changing environmental temperature and shortage of food are not associated with increased laboratory flight. However, a contribution of crowding cannot be excluded, particularly if it were to be present in conjunction with decreasing photoperiod.

This study provides an important overview of *C. molesta*'s developmental response to a number of factors synchronous with the peach to apple host shift and has generated significant baseline data from which to generate testable hypotheses on interorchard dispersal of *C. molesta.* A previous laboratory flight investigation indicated that female *C. molesta* are the main dispersers of this species (Hughes and Dorn 2002), and this is also indicated in this study. Such dispersal is part of a suite of covarying traits that evolves as a consequence of adaptations for successful colonization (Rankin and Burchstead 1992), and other stimuli, including food quality reduction, may also be involved in *C. molesta* dispersal. Most recent studies indicate that host plant volatiles can be ruled out as stimuli promoting the host shift from peach to apple, because no preferences of female moths were detected for apple volatiles (Natale et al. 2003a, b).

This elucidation of the relative importance of key elements inducing *C. molesta* dispersal to apples will allow better estimation of the core migrational period and consequently improve timing of pest management measures within an integrated pest management framework. Photoperiod is highly predictable and therefore is a reliable indicator for the time when surveillance of moths immigrating into pome fruit orchards should begin. Furthermore, this study has contributed to filling a major gap in knowledge on the influence of preimaginal environment on the dispersal of an economically important tortricid pest.

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